physical conditions. We have based this discussion upon North American types because the physical aspect of the barriers are not so pronounced as in some other parts of the world and because we wished to emphasize the psychological aspect of these barriers. Although the writer knows nothing of the biological problem that has been discussed in these pages, he ventures to suggest that the habits of animals formed in response to environmental conditions may become psychological barriers to diffusion. There may be a kind of psychophysical at-home feeling that ties a species to certain areas.

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SPECIAL ARTICLES.

PHYSIOLOGICAL REGENERATION IN INSECTS.

MORGAN in 'Regeneration' (1901), p. 19, defines physiological regeneration as follows:

> Finally, there are certain normal changes that occur in animals and plants that are not the result of injury to the organism, and these have many points in common with the processes of regeneration. They are generally spoken of as processes of physiological regeneration. The annual moulting of the feathers of birds, the periodic loss and growth of the horns of stags, the breaking down of cells in the different parts of the body after they have been active for a time, and their replacement by new cells, the loss of the peristome in the protozoon, *Stentor*, and its renewal by a new peristome, are examples of physiological regeneration. This group of phenomena must also be included under the term 'regeneration' since it is not so sharply separated from that including those cases of regeneration after injury, or loss of a part, and both processes appear to involve the same factors.

Again, on p. 25 (*ibid.*), Morgan says that he will use the term physiological regeneration to include such changes "as the moulting and replacement of the feathers of birds, the replacement of teeth, etc.—changes that are a part of the life-cycle of the individual. In some cases it can be shown that these processes are clearly related to ordinary regeneration, as when a feather pulled out is formed anew without waiting for the next moulting period, and formed presumably out of the same rudiment that would have made the new feather in the ordinary moulting process."

Finally, on pp. 128–131 (*ibid.*), Morgan refers to the general fact that 'in the same animal certain organs may be continually worn away and as slowly replaced, and other organs replaced only at regular intervals,' and he lists a number of familiar instances of regularly recurring physiological regeneration, as the moulting of snakes, the throwing off of deer antlers and their renewing, and also the moulting of insects. As this is the only instance of physiological regeneration in insects mentioned by the author, and as it seems to be desirable to know, especially as a basis for any discussion of the relation between 'physiological regeneration' and the more familiar restorative phenomenon called simply 'regeneration,' of any other instances of physiological regeneration occurring among the lower animals—almost all the cited cases of physiological regeneration are among the vertebrates—I wish to point out briefly certain important and widespread phenomena in insect biology which should be included in the category of physiological regeneration processes. Indeed, Morgan specifically refers to the need of such further knowledge. "How far," he says, "physiological regeneration takes place in the tissues of the lower animals we do not know at present except in a few cases, but far from supposing it to be absent, it may be as well developed as in higher forms."

First may be mentioned the radical regeneration of the digestive epithelium of the ventriculus, common to all (?) insects, a phenomenon long known, albeit in a rather hazy way perhaps, to students of insect morphology, but in the last ten years carefully studied and satisfactorily worked out for a number of insect forms representing several widely separated orders. (See the papers of Mobusz, Rengel, Van Gehuchten, Needham and others.) This process consists of the constant senescence and complete degeneration of the nuclei and cytoplasm of the large epithelial cells of the ventricular portion of the alimentary canal and of the equally constant appearance of new nuclei in conspicuous small

groups or 'nests' near the basal membrane, their increase in size (growth) and migration toward the lumen, with an accompanying new formation of surrounding cytoplasm. The vigor of nucleus and cytoplasm seems to be exhausted after the secretion and discharge of a certain amount of digestive fluid, and rapid and perfectly obvious senescence and histolysis take place. Inspection of cross-sections of the ventriculus of any feeding caterpillar will show this normal physiological regeneration phenomenon in most illuminating manner. While this regenerative process was, when first noted, considered to be a part of that extensive general histolysis and histogenesis which regularly accompanies the post-embryonic development of insects with 'complete metamorphosis,' it is now known—thanks especially to Needham's discriminating work—to be a phenomenon also accompanying or incident to digestion, occurring all through the feeding life of the insect, and not limited to that period in late larval life (pre-pupal life) when the radical histolysis of the larval organs occurs, preparatory to, or coincident with, the new-building (histogenesis) of the imaginal (adult) organs. There is, however, probably always a marked and unusual degree of regeneration of alimentary epithelium during the prepupal and early pupal stages, *i. e.*, at the time of the radical transformation phenomena. This has been recently well shown in the case of the water-beetle *Cybister*, by Degeener.[1]

A more striking phenomenon, or group of phenomena, of physiological regeneration in insects is that extraordinary double process of degeneration and moulting on the one hand and regeneration and complete new-building on the other which characterizes the ontogeny (in post-embryonic life) of the insects with so-called 'complete metamorphosis,' *i. e.*, those insects which come from the egg in a form (larva) radically different from that of the definitive adult condition. From the butterfly's egg there hatches a caterpillar without wings, without compound eyes, with eight pairs of legs, with minute, short two- or three-segmented antennæ, with biting and chewing mouth-parts composed of heavy mandibles, jaw-like maxillæ, and flap-like labium, with musculature for worm-like and creeping locomotion, and with simple, straight alimentary canal for the manipulation and digestion of bits of solid food (leaves, etc.). But the butterfly into which the caterpillar develops has wings, compound eyes, long, many-segmented antennæ, only three pairs of legs, sucking mouth-parts composed of a curious long flexible tube made up of the maxillæ alone, with mandibles wholly wanting and labium reduced to a small fixed sclerite, complex musculature for flight, and a long twisted alimentary canal with conspicuous sac-like diverticula for holding and digesting flower nectar. In even greater degree do the larva and adult of the Diptera and Hymenoptera differ, and in only slightly less degree those of the Neuroptera and Coleoptera. Now in all these specialized insects the development from larva to adult (usually achieved in a few days or weeks) is not accomplished by a slow, gradual transformation of the parts of the larva into those of the adult, but is distinguished by the curious fact that many, if not most, of the larval organs are either wholly cast aside by moulting at the time of pupation, or undergo a radical histolysis resulting in complete disintegration. The larval mouth parts and antennæ are completely discarded at pupation (last larval moulting) and have their places taken by wholly new and usually markedly different mouth parts and antennæ; the larval musculation, parts or the whole of the alimentary canal, the salivary glands and Malpighian tubules, and parts or the whole of the tracheal system degenerate, and have their places taken by radically new muscles, alimentary canal, salivary glands, Malpighian tubules and tracheæ, produced (regenerated) from elementary cell groups called histoblasts or imaginal buds. This phenomenon of wholesale histolysis and histogenesis characteristic of all the members of all the orders of insects with complete metamorphosis (with some Coleoptera and some Neuroptera the breakdown and new-building is slight) is to be looked on as a wholesale and extreme case of

[1] *Zool. Jahrb.*, v. 20, pp. 499–676, 1904.

physiological regeneration. It is a normal part of the ontogeny of these specialized insects, but it is an interpolated, a cænogenetic condition. That is, although now a regularly recurring phenomenon in the life of these insects, it is distinguished only by the inevitableness and regularity of its occurrence from any occasional processes involving profound regeneration. It seems to me quite analogous with such cases of regularly recurring physiological regeneration as the moulting and new-growth of the plumage of birds, the casting off and new-building of the antlers of stags, the loss of the peristome and the formation of a new one in *Stentor*, etc.; in other words, with all those cases mentioned by Morgan in illustration of his definition of physiological regeneration.

In the two special cases of physiological regeneration in insects here called attention to, we may distinguish between regeneration of the ventricular epithelium from tissue (cells) of its same kind, and the regeneration of wings, legs, mouth parts and antennæ from cells not belonging to similar organs but simply forming part of the continuous larval derm. In this latter case of regeneration, too, the 'regenerated' parts are in all cases different from preexisting parts and in some cases (wings, for example) are wholly new parts. One might say that this is not regeneration at all, but simply development (ontogeny). But in numerous cases of true restorative regeneration the new parts do not agree exactly with the replaced ones; often they are markedly smaller, they lack segments, they lack many details; they are cases of teratogenesis. For example, the cockroaches (Blattidæ) have the capacity of regenerating lost legs, or rather parts of legs; but whereas the normal leg has always five tarsal segments, the regenerated one has always four. All regeneration may, of course, be looked on as a phenomenon of ontogeny; a regulation. In practically all animals which can regenerate at all, the capacity for regeneration is much greater in immature life than in adult life: in many, indeed, it exists only in the immature stages.

In connection with this brief reference to the occurrence of physiological regeneration in insects, it may not be amiss to refer, even more briefly, to our present knowledge of ordinary or what is called, for the sake of a provisional distinction between the two categories, restorative or accidental regeneration among insects. It has long been known that certain insects of incomplete metamorphosis, notably many Orthoptera, have the power of regenerating lost parts of legs, antennæ and certain other externally produced organs, as tracheal gills. Associated with this regenerative capacity occurs, in some insects, at least, self-mutilation or autotomy. In addition, it has also long been known that if the legs or antennæ be cut off from the larva of certain insects with complete metamorphosis (moths, beetles and others) the adult will appear with 'regenerated' legs or antennæ, sometimes perfectly normal in size and form, sometimes normal in form but reduced in size, and other times abnormal (usually lacking distal parts) in form. But, as I have already pointed out in a paper on the regeneration of the larval legs of silkworms,[2] this latter kind of 'regeneration' may not be restorative regeneration at all, but a phenomenon of physiological regeneration incident to the regular process of development of the imaginal legs, antennæ, etc., of insects of complete metamorphosis in the course of which the larval organs disintegrate and the imaginal ones get formed from histoblasts which lie in such position, at least in early larval life, as to be uninjured by any cutting of the larval legs. Finally, as I have shown in the paper just referred to, the larvæ of at least one species of moth, *Bombyx mori*, have the capacity of regenerating during larval life both thoracic (jointed) legs and abdominal (prop) legs. Tornier[3] also states that the larvæ of the meal worm, *Tenebrio molitor*, can also regenerate, before pupation, cut off legs, or parts of legs.[4]

[2] *Jour. of Exper. Zool.*, Vol. I., pp. 593–599, 1904.

[3] *Zool. Anzeig.*, Vol. 24, 1901.

[4] For accounts giving reviews and bibliography, in some degree of completeness, of the recorded cases of experiments and observations of regeneration, in insects, see Brindley, 'On Certain Char-

Because of the importance that regenerative phenomena have in the consideration of certain fundamental biologic problems, one might be tempted to try to find some significance in whatever special examples of regeneration happen to come under one's own observation. The relation between physiological regeneration and restorative regeneration is a subject very near at hand, if one were to look for something to speculate about in connection with what I have noted in this paper on regeneration in insects. But with Morgan, it seems to me that 'we do not gain any insight into either of the processes, so far as I can see, by deriving one from the other, for the process of restorative regeneration may be in point of time as old as that of physiological regeneration.' Indeed, among the insects we have good grounds for believing restorative regeneration older than the particular processes of physiological regeneration which regularly accompany the post-embryonic development of insects with complete metamorphosis. For these insects are admittedly the recent, the post-Tertiary, ones, while the Orthoptera, among which, especially, restorative regeneration is widespread and unusually well developed, are among the oldest of living insect orders. They make up the bulk of insects known from pre-Tertiary times. The most extensive and radical of physiological regeneration processes occur precisely among the most specialized, the most recent, insects.

Finally, as concerns the large question of whether regeneration is to be looked on as a certain primary, primitive, attribute of organisms whose manifestation becomes weaker as complexity in structure and function is attained (in course of descent), or whether, as is held by the Neo-Darwinians, it is to be looked on as an adaptation which has been transmitted through a long and many-branched course of descent, gradually weakening during this transmission until in the more complex organisms it is largely lost, although, in consonance with need, often retained even among higher forms, this is a question I shall refer to only in so far as to say that the evidence presented by all that we know of regeneration in insects, taken together, certainly does not warrant any such definite conclusion as Tornier expresses on the basis of his experiments with certain dragon-fly and May-fly larvæ, viz., that regeneration in insects is an adaptation produced by natural selection.

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acters of Reproduced Appendages in Arthropoda, Particularly in the Blattidæ,' *Proc. Zool. Soc. London*, 1898, pp. 924–928; and Tornier, *Zool. Anzeig.*, Vol. 24, 1901, pp. 634–664.

A PRELIMINARY NOTE ON ASCUS AND SPORE FORMATION IN THE LABOULBENIACEÆ.

CONCERNING the systematic position of the Laboulbeniaceæ many opinions have been expressed. DeBary (1884) included them in his doubtful Ascomycetes; Thaxter (1895), of all best qualified to speak, referred them to the Ascomycetes; Karsten (1895) maintained that they were not Ascomycetes at all, but that they occupied a position intermediate between the smuts and the Pyrenomycetineæ, while Engler ('Syllabus der Pflanzenfamilien,' 1903) has elevated them to the rank of a class quite removed from both the smuts and the Ascomycetes. These differences in opinion have arisen from a lack of knowledge of the actual phenomena of spore production, a gap due to difficulties in obtaining and manipulating material suitable for cytological investigation.

In the course of recent investigations on the Ascomycetes I have given some attention to these peculiar and interesting forms, and an examination of microtome sections of well-preserved perithecia has revealed features that are apparently of undoubted significance in their bearing on the problem of the phylogenetic position of this group.

As for the spore sac, it has been discovered that each is primarily occupied by a fusion nucleus. Three successive nuclear divisions follow. The spore initials are delimited from an abundant epiplasm under the superintendence of the last generation of nuclei. The young spores are bounded by a plasma membrane, and the cavities in the epiplasm in which they lie are lined by a membrane of similar character. Indeed, the phenomena of